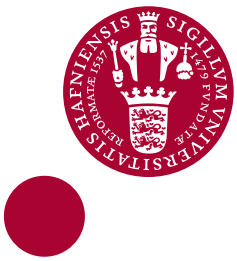

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Meta-networks for the study of biogeographical traits in ecological networks: the Mexican hummingbird-plant assemblage

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Abstract

Recent studies on ecological networks have quantified the contribution of ecological, historical and evolutionary factors on the structure of local communities of interacting species. However, the influence of species' biogeographical traits, such as migratory habits or phylogeographical history, on ecological networks is poorly understood. Meta-networks, i.e. networks that cover large spatial extensions and include species not co-occurring locally, enable us to investigate mechanisms that operate at larger spatial scales such as migratory patterns or phylogeographical distributions, as well as indirect relationships among species through shared partners. Using a meta-network of hummingbird-plant interaction across Mexico we illustrate the usefulness of this approach by investigating (1) how biogeographical and morphological factors associate with observed interactions, and (2) how species-specific biogeographical characteristics associate with species' network roles. Our results show that all studied hummingbird and plant species in the meta-network were interrelated, either directly or through shared partners. The meta-network was structured into modules, resulting from hummingbirds and plants interacting preferentially with subsets of species, which differed in biogeographical, and, to a lesser extent, morphological traits. Furthermore, migrants and hummingbirds from Nearctic, Transition and widespread regions had a higher topological importance in the meta-network. Taken together, this study illustrates how meta-networks may contribute to our current knowledge on species biogeographical traits and biotic interactions, providing a perspective complementary to local-scale networks.

Keywords biotic interactions, migration, modularity, morphology, phylogeny, pollination

INTRODUCTION

Species interactions, such as pollination and other mutualistic associations, are widespread and crucial for the functioning of most ecological communities (Rech et al. 2016). An urgent challenge in ecology amidst global change is to quantify the contribution of ecological, historical, evolutionary and biogeographic mechanisms in the structuring of communities of interacting species (Ricklefs 1987; Cavender-Bares et al. 2009; Martín González et al. 2015; Heilmann-Clausen et al. 2017; Dalsgaard et al. 2018). This is a complex subject, as species typically show a context-dependent behavior reflecting their adaptation to a mosaic of factors presented in their local communities, which in turn interplay at different scales. Hence, the need of using a wide set of complementary analyses to study the effect of different factors and at different scales (Thuillier et al. 2013; Poisot et al. 2015). For instance, the study of interactions between plants and their pollinators over different seasons and years, including species whose phenophases may not fully overlap, has enabled us to explore the effect of climate, resource seasonality and species phenophases on community structure and species' roles. Besides a more accurate understanding of community structure and build up, these networks allow us to characterize more accurate the role of species and potential fluctuations over time (Martín González et al. 2012; Chacoff et al. 2017, Kantsa et al. 2018). Similarly, the study of "meta-networks", i.e. networks of biotic interactions covering large spatial scales, across biomes or in fragmented habitats, may give new insights into how species biogeographical traits such as phylogeographical distribution, range dynamics or migratory habits influence ecological networks, of which there is scarce knowledge (Heilmann-Clausen et al. 2016; Araujo et al., 2018; Emer et al. 2018).

Meta-networks enable us to study indirect interactions among species, that is, relationships between species that do not co-occur spatially or temporally, but which may have an effect on each other through third species. For instance, two consumer species whose ranges may not overlap currently but which visit a similar array of resources, and hence may prevent the expansion into each other ranges. Hence, the study of meta-networks may be particularly useful to understand landscape dynamics, such as the effect of biotic interactions on range dynamics (e.g. Araújo and Luoto 2007), and the role and importance of species which,

because of large spatial distributions (e.g. migrant species), may appear as peripheral in local networks due a lower detection probability (Vázquez et al. 2009).

Biogeographical factors may be especially important in areas with a complex geography and topography, in contact zones between biogeographical realms and in areas with communities containing species with large differences in range distributions or migratory habits. An outstanding combination of such factors is the Mexican hummingbird-plant assemblage. Mexico is located at the transition between the Nearctic and Neotropical realms (Halffter 1987; Rzedowski 1965), and exhibits a complex topography and geological history (Morrone 2010; Morrone et al. 2017; Fig. 1). Its wide array of ecological conditions has favoured population isolation and the action of *in situ* evolutionary processes (Navarro et al. 2002), enabling to find fauna, largely endemic, with different biogeographical and evolutionary origins. For instance, the Mexican hummingbird fauna appears to have arisen from multiple independent invasions of different phylogenetic lineages and at different times (Stiles 1981; Brown and Bowers 1985; Bleiweiss 1998; Licona-Vera and Ornelas 2017; see more details in methods). Several of the Mexican hummingbirds have very particular biogeographical and ecological restrictions, which entails both processes of diversification and endemism (Rodríguez-Gómez et al. 2013; Malpica and Ornelas 2014; Licona-Vera and Ornelas 2014; Ornelas et al. 2015). For instance, most of the 24 endemic Mexican hummingbirds are restricted to regions of narrow extensions, little landscape connectivity, and complex topography and floral composition. Furthermore, the Mexican hummingbird fauna includes a mixture of sedentary, altitudinal and short-distance migrants who track nectar availability of local resources, and obligate seasonal long-distance migrants who have latitudinally different winter and breeding grounds (e.g. Lara 2006; Licona-Vera and Ornelas 2017).

Hence, given the large differences phylogeographical history, range distributions and migratory habits among Mexican species, we expect these biogeographical traits to exert a strong effect on hummingbird-plant interactions and, therefore, on network structure. However, most studies on hummingbird-plant assemblages have focused exclusively on the effect of morphological traits, which have been shown to regulate interactions in some but not

all communities (e.g. Maglianesi et al. 2014, 2015; Vizentin-Bugoni et al. 2014; Weinstein and Graham 2017; Dalsgaard et al. 2018). For instance, in the Brazilian Cerrado hummingbird traits have been shown to produce modules within local networks with their nectar-food plants (Maruyama et al. 2014). On the other hand, the role of biogeographical traits remains less well known (Sonne et al. 2016; Araujo et al. 2018). In this study we investigate the role of hummingbird's biogeographical and morphological traits in structuring a meta-network comprising all available information on hummingbird-plant interaction across Mexico. We expect that the Mexican meta-network will show a strong modular pattern in which modules can be interpreted in terms of species' biogeographical traits, an analogous outcome to the modular pattern of highly seasonal mutualistic assemblages where modules reflect species' staggered phenophases (Martín González et al. 2012). Specifically, we investigate (1) how hummingbird's biogeographical and morphological traits associate with the modular partition, and (2) how hummingbird's biogeographical and morphological traits may associate with the network role of hummingbirds in the meta-network.

Methods

Study area and study species

Mexico is an outstanding example of complex biogeographical patterns (Morrone 2010; Morrone et al. 2017). The country currently stands out as a mega-diverse country, likely a consequence of its location at the transition between the Nearctic and Neotropical realms (Halffter 1964, 1987; Rzedowski 1965, 1992) and the close relationship between geological/climatic and speciation events (Croizat 1958, 1964; Rosen 1978; Halffter 1987; Liebherr 1991; Luna-Vega et al. 1999). In Mexico, the Nearctic realm comprises the arid subtropical areas that extend from northern to the high plateaus along the Volcanic Belt and the Sierras Madre, where it intermixes broadly with the Neotropical realm which includes humid and subhumid tropical areas in the central-south part of the country (Halffter 1964; Morrone and Márquez 2001; Morrone et al. 2017; Fig. 1).

Hummingbirds (Trochilidae) are the most highly specialized nectarivorous birds in the New World, relying almost exclusively on nectar as a food source (Stiles 1981). They distribute from Alaska through Patagonia, and their interactions with plants show strong biogeographical and evolutionary patterns, ranging from generalized to highly specialized (Stiles 1978; Dalsgaard et al. 2009, 2011; Abrahamczyk and Kessler 2014; Martín González et al. 2015; Sonne et al. 2016). Their adaptive radiation manifests them as a highly diverse clade, with more than 338 described species (McGuire et al. 2014). With approximately 58 recognized species, Mexico hosts 17% of the described hummingbird species. The Mexican hummingbird fauna is relatively recent and results from various colonization waves from South America (McGuire et al. 2014; Ornelas et al. 2014). The high habitat diversity and abrupt environmental and climatic changes that characterize Mexico have played a key role on processes of divergence and speciation, resulting in a great level of endemism and varied migratory habits of Mexican hummingbirds (Malpica and Ornelas 2014; Licona-Vera and Ornelas 2017; Appendix 1).

Interaction data and species traits

We compiled 37 hummingbird-plant interaction networks describing feeding relationships between hummingbirds and plants throughout Mexico, spanning over nine different habitats and ten biogeographic provinces (as defined by Morrone et al. 2017), including both Neotropical and Nearctic realms and the Transition zone (Fig. 1, coordinates and references for details on Appendix 2). Overall, we compiled information on hummingbird visitation for 41 hummingbird species and 354 plant species, covering all but three of the nine taxonomically recognized phylogenetic lineages (McGuire et al. 2014) and comprising a wide range of body masses (2.5–11.9 g) and bill lengths (11.3–43.2 mm). Hummingbirds were classified following Escalante et al. (1993) as endemic, when their entire distribution is restricted to Mexico (8 species); semi-endemic, when the entire population is seasonally present in Mexico or in narrowly overlapping adjacent countries (<35000Km^2; 9 species); and non-endemic (24 species). Some hummingbirds have long-distance migratory habits (7 species), others migrate locally (9 species) and others are year residents (25 species;

Arizmendi and Berlanga 2014). The biogeographical distribution of hummingbirds was categorized as Nearctical, when the hummingbird was reported only in Nearctical or in Nearctical and Transition localities (6 species), as Neotropical when the hummingbird was reported only in Neotropical or in Neotropical and Transition localities (16 species), as Transition, when the hummingbird was reported only in Transition localities (8 species), or widespread if the hummingbird was present in Nearctical, Neotropical and Transition regions (11 species; Table 1). Plants belong to 66 different families, are mostly native species (271 species, 92% of total) and include both typical ornithophilous and non-ornithophilous floral morphologies (see Appendix 2 for a list of plants present in the meta-network).

Meta-network analyses

To investigate the structure of the Mexican meta-network, we merged all information on the presence/absence of species interactions into a single meta-network describing whether each hummingbird and plant species interacted anywhere in Mexico (Appendix 2). We thereafter examined the potential modularity of this meta-network. Modularity was calculated in MODULAR (Marquitti et al. 2014) using Barber's metric for bipartite networks (Barber 2007), with simulated annealing as the searching algorithm and following the recommended program settings (Marquitti et al. 2014; Appendix 3). Barber's modularity divides the matrix into an a priori undefined number of modules using matrix's eigenvalues, minimizing the number of links between modules while maximizing within-module connectance (Barber 2007). Hence, in the resulting partition, species located in the same module interact more among themselves than with species from other modules. As MODULAR uses an iterative searching algorithm, we investigated the robustness of the resulting modular partition by running the analysis 30 times using different seed set numbers. In addition, we estimated the significance of each run against 100 null matrices obtained with MODULAR's Null Model 2, which creates matrices with the same number of species and interactions as the empirical one, and in which species interaction probability is based on their observed connectivity (Bascompte et al. 2003; Marquitti et al. 2014).

We examined the resulting modular partition in order to understand the underlying mechanisms associated with such pattern of interactions. We performed a non-metric multidimensional scaling (NMDS) of hummingbird morphological and biogeographical traits known or hypothesized to associate with hummingbird-plant interactions, namely bill length, body mass, degree of endemicity, migratory habits and biogeographical distribution. The NMDS was run following the approach recommended in the R package *vegan* (Oksanen et al. 2017), e.g. the ordination was run 5 times, with a minimum number of 200 iterations and using the previous best solution as starting point. To the resulting ordination, we fit a secondary matrix, which included group membership (e.g. which groups of hummingbirds were found in the same modules in the different runs of the modularity algorithm) and phylogenetic lineage as factors. Hence, we tested whether species from different groups or from different hummingbird phylogenetic lineages show different morphological or biogeographical traits.

Finally, from the resulting modular partition we obtained information on the network role of each hummingbird species by computing species' within-module degree (*z-values*) and among-module connectivity (*c-values*) in the *cz*-values function from the R package *bipartite* (Dormann 2012). Within and among module connectivities are calculated as $z = (k_{is} - ks_{bar}) / SD_{ks}$ and $c = 1 - \Sigma (k_{it}/k_i)^2$, respectively, where k_i is the degree of focal species *i*; k_{is} is the degree of focal species *i* to the rest of the species within *i*'s module; ks_{bar} is the average degree of all species in module *s*; SD_{ks} is the standard deviation of the degrees of species in module *s*; and k_{it} is the number of links of focal species *i* to species located in module *t* (Olesen et al. 2007; Dormann 2012). Hummingbirds can therefore be classified according to how their interactions distributed within and across modules as *hubs* when their z-values are high; as *connectors,* when their c-values are high; and as *peripherals,* when they are poorly connected and only within their module, and hence both their *c* and *z-values* are small. As hummingbird traits were a mixture of continuous (bill length and body mass), categorical ordered (degree of endemicity and migratory habits) and categorical unordered variables (biogeographical distribution), we used a non-parametric multiple regression with kernel estimation to examine

222 whether their *z* and *c-values* associate with any of these traits, using the R package *np* (Hayfield and Racine 2017). All statistical analyses were performed in R 3.3.1 (R
224 Development Core Team 2014).

226 **Results**

The meta-network consisted of 395 species and 1128 interactions, and had a connectance of
228 8%. All species conformed the giant component, that is, there were no separate subnetworks of species. The two most distant species in the meta-network were seven edges apart, while
230 the average number of shortest paths between any two species in the meta-network was 3.389. Different runs of the MODULAR algorithm yielded different though relatively constant
232 modularity values ($M = 0.466 \pm 0.004$), all of which were highly significant when compared to null models (all p-values <0.001; Appendix 3). Despite resulting partitions varied between
234 five and eight different modules, species composition of modules was relatively constant, with all but five of the hummingbird species being placed over 87% of the runs together in the
236 same module (that is, in 26 out of the 30 runs of the modularity algorithm; Fig. 2; group species compositions are given in Appendix 2; results from the modularity analysis are given
238 in Appendix 3).

240 The NMDS analysis on the morphological and biogeographical traits of the 41 hummingbird species of the meta-network resulted in a two-dimensional solution with a stress value of
242 0.132 (Fig. 3). In axis 1 morphological traits and biogeographical distribution had positive scores whereas degree of endemism and migratory behavior had negative scores. The
244 strongest associations were, in this order, with hummingbird migratory behavior and biogeographical distribution. All variables were negatively associated with axis 2 except for
246 endemism, which was also the trait with the highest score, followed by bill length and body mass. Moreover, the resulting ordination was significantly correlated with hummingbird
248 module composition ($R^2 = 0.426$, $p = 0.001$), that is, modules differed in the traits analyzed in the NMDS.

250

The two non-parametric multiple regressions performed between the *z*- and *c-values* and hummingbird traits resulted in strong and statistically significant associations (Table 2, Appendix 4). The *z*- and *c-values* were averaged across runs as different runs of the modularity algorithm yielded different partitions as species *z*- and *c-values* differed: range SD = 0.038–0.94 and 0.00–2.36 for *z* and *c-values*, respectively. Migratory behavior and biogeographical distribution showed a highly significant association with both *z* and *c-values* (Table 2, Fig. 4), with migratory and Nearctic/Widespread species showing higher within and among module connectivity values than non-migrants and Neotropical hummingbirds. Hummingbird *z-values* also correlated negatively with bill length and body mass, that is, large and long-bill hummingbirds tend to have a peripheral position in the meta-network (Table 2, Fig. 4).

Discussion

In this study we explore the usefulness of meta-networks to investigate the effect of biogeographical traits on species interactions. In order to do so, we chose a study system of high geological complexity such as Mexico and a bird group model, which is broadly distributed and shows a wide array of biogeographical and morphological traits that may influence their interaction pattern with plants. By studying the Mexican hummingbird-plant assemblage at a macroecological scale, we included direct and indirect interactions among species. The resulting meta-network was fully connected; this indicates that all studied species had the capacity of influencing each other, even when not co-occurring at the same localities. Moreover, the average shortest path length of 3.389 indicates that even indirect interactions may exert relatively strong influences across the network. The meta-network was also highly modular, with modules reflecting differences in the migratory habits and degree of endemicity of hummingbirds.

Our results highlight the large importance of migratory hummingbird species in the structure of the meta-network. Migration in Mexican hummingbirds appears to be a highly labile and relatively recent trait, occurring repeatedly and independently on several species from basal

sedentary ancestors (Licona-Vera and Ornelas 2017). Migratory hummingbirds have significantly higher *c-values*, that is, a relatively high proportion of their interactions are with plant species from other modules, increasing overall network cohesiveness (Olesen et al. 2007; Tylianakis et al. 2010; Stouffer and Bascompte 2011) and the potential importance of indirect interactions. In highly seasonal pollination networks this role is achieved by pollinator species with long phenophases, who connected species with much more restricted activity periods (Martín González et al. 2012; Kantsa et al. 2018). Modular networks are expected to be highly resilient, as disturbances are less likely to spread beyond modules (Olesen et al. 2007; Tylianakis et al. 2010; Stouffer and Bascompte 2011). However, at the same time, this particular topological configuration renders connectors a foremost importance, as they are able to affect rapidly the rest of the species in the network. Migratory Mexican hummingbirds show an interaction behavior relatively robust to changes in habitat conditions and in plant distributions and phenologies. By experimentally simulating changes in the environment, Ornelas and Lara (2015) showed that some migratory Mexican hummingbird species included in this study (i.e. Emerald *Amazilia beryllina* and Bee *Selasphorus rufus*) are able to quickly change and adjust their colour preferences of the flowers they visit due to the short time spent in a given novel environment, whereas resident hummingbirds also included in this study (i.e. Emerald *Hylocharis leucotis* and Gem *Lampornis amethystinus*) usually prefer visiting their natural red flower type and they take longer to change their colour preferences. This apparent neophilia in the migratory hummingbirds could favor the easy incorporation of non-familiar resources, such as invasive plant species, into their interaction networks.

The biogeographical distribution of species was strongly associated with the role of species in the network. Nearctic, Transition and widespread hummingbirds showed a higher within-module and among-module connectivity. Most of these hummingbirds are also migrants (Table 1), and hence have wider range distributions and habitat preferences. Another possible explanation for the higher importance of Nearctic and widespread hummingbirds involves the divergence time of hummingbirds and their floral preferences. For example, hummingbird species from the Bees and Mountain Gems clades are distributed particularly in North

America and Central America (mostly in the Nearctic realm), being the only lineages that expanded and diversified in these regions (~12 million years ago, McGuire et al. 2014; Licona-Vera and Ornelas 2017) and show a significantly higher mean *c-value* (Appendix 5). Altogether, these species seem to be more evolutionary and ecologically dynamic. In contrast, Neotropical clades such as Hermits (e.g. *Phaethornis* spp.) and Emeralds (e.g. *Amazilia* spp.) had more recent invasions from South America and a subsequent diversification in the Mesoamerican zone (Ornelas et al. 2014), and have a more peripheral role in the meta-network.

The most common ancestral condition for the hummingbird flowers of North America is a bee-pollinated system (Grant and Grant 1968), promoting hummingbirds to be particularly generalist in their interactions with plants in the Nearctic realm. North-American hummingbirds have a closer phenotype than other hummingbird assemblages (Stiles 1981; Brown and Bowers 1985), which also translates into a higher congruence in the floral phenotypes. By contrast, ornithophilous genera of plants are centred in subtropical or tropical America, where hummingbird-plant interactions show higher levels of specialization and morphological complementarity (Stiles 1978; Dalsgaard et al. 2011). Hence, in Mexican hummingbird-plant assemblages, morphological traits may be, *a priori*, not as important as other mechanisms in structuring interactions at the community level. Our results show that both the length of the bill and the body mass of the hummingbirds affect the number of interactions hummingbirds establish within their module, with short-bill and smaller species showing a tendency to interact with a higher number of plants within their modules than long-bill and larger hummingbirds. Long bills restrict the number of plants from which a hummingbird can effectively extract nectar, while larger hummingbirds have higher energetic demands which constrain their available floral choices to flowers providing mid-high amounts of nectar, of which the North American flora is relatively scarce (Stiles 1981; Brown and Bowers 1985). Hence, in the Mexican hummingbird-plant assemblage there seems to be a preference for not establishing strong morphological or energetic barriers between hummingbirds and their nectar plants.

Taken together, our study of the Mexican hummingbird-plant meta-network illustrates how meta-networks may provide a more complete view on the dynamics of ecological communities, particularly as the importance and behavior of migrant species may not be fully characterize when studying only local-scale networks. Notably, through a meta-network, we have been able to capture the direct and indirect interactions between hummingbirds and their nectar plants across Mexico, resulting in relevant insights on the importance of biogeographical traits for such assemblages. This emphasizes the usefulness of meta-networks for the characterization of the factors shaping species communities and how they interact across large spatial scales. This approach may be extended to other taxa and biogeographical regions, and may prove valuable in order to asses the effects of mechanisms that operate at large spatial scales such as habitat fragmentation, species invasions, the effect of biotic interactions on range dynamics and changes in species phenophases (Araújo and Luoto 2007; Araujo et al. 2018; Emer et al. 2018).

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References

Abrahamczyk S, Kessler M (2014) Morphological and behavioural adaptations to feed on nectar: how feeding ecology determines the diversity and composition of hummingbird assemblages. J Ornithol 156:333–347

Araujo AC, Martín González AM, et al. (2018) Spatial distance and climate determine modularity in a cross-biomes plant-hummingbird interaction network in Brazil. J Biogeogr, in press.

370 Araújo MB, Luoto M (2007) The importance of biotic interactions for modelling species distributions under climate change. Glob Ecol Biogeogr 16:743–753

372 Arizmendi MC, Berlanga H (2014) Colibríes de México y Norteamérica / Hummingbirds of Mexico and North America. CONABIO Mexico

374 Barber MJ (2007) Modularity and community detection in bipartite networks. Phys Rev E 76:066102

376 Barber BR, Klicka J (2010) Two pulses of diversification across the Isthmus of Tehuantepec in a montane Mexican bird fauna. Proc R Soc B 20100343

378 Barrier E, Velasquillo L, Chávez M, Gaulon R (1998) Neotectonic evolution of the Isthmus of Tehuantepec (southeastern Mexico). Tectonophysics 287:77–96

380 Bleiweiss R (1998) Origin of hummingbird faunas. Biol J Linn Soc 65:77–97

Brown JH, Bowers MA (1985) Community organization in hummingbirds: relationships
382 between morphology and ecology. The Auk 102:251–269

Cavender-Bares J, Kozak KH, Fine PV, Kembel SW (2009) The merging of community
384 ecology and phylogenetic biology. Ecol Lett 12:693–715

Chacoff N, Resasco J, Vázquez DP (2017) Interaction frequency, network position, and the
386 temporal persistence of interactions in a plant-pollinator network. Ecology 99:21–28

Cotton PA (2007) Seasonal resource tracking by Amazonian hummingbirds. Ibis 149:135–
388 142

Dalsgaard B, Martín González AM, Olesen JM, Ollerton J, Timmermann A, Andersen LH,
390 Tossas AG (2009) Plant-hummingbird interactions in the West Indies: floral specialisation gradients associated with environment and hummingbird size.
392 Oecologia 159:757–766

Dalsgaard B, Magård E, et al. (2011) Specialization in plant-hummingbird networks is
394 associated with species richness, contemporary precipitation and quaternary climate-change velocity. PLoS One 6:e25891

396 Dalsgaard, B, Kennedy, JD, et al. (2018). Trait evolution, resource specialisation and vulnerability to plant extinctions among Antillean hummingbirds. Proc R Soc B: 398 20172754

Dormann CF (2012) Visualising bipartite networks and calculating some (ecological) indices. 400 Package "bipartite"

Emer C, Galetti M, Pizo MA, Guimarães PR, Moraes S, Piratelli A, Jordano P (2018) Seed-402 dispersal interactions in fragmented landscapes – a metanetwork approach. Ecol Lett 21:484–493

404 Escalante P, Navarro AG, Peterson AT (1993) A geographic, historical and ecological analysis of land bird diversity in Mexico. In: Ramamoorthy TP, Bye R, Fa J, Lot A 406 (eds) Biological diversity in Mexico: Origins and distributions. Oxford University Press, New York, pp 281–307

408 Gómez-Tuena A, Orozco-Esquivel MT, Ferrari L (2005) Petrogénesis ígnea de la faja volcánica transmexicana. Bol Soc Geol Mex 57:227–283

410 Gómez-Tuena A, Orozco-Esquivel MT, Ferrari L (2007) Igneous petrogenesis of the Trans-Mexican Volcanic Belt. Geol Soc Am 422:129–181

412 Grant KA, Grant V (1968) *Hummingbirds and their flowers*. Columbia University Press.

Hayfield T, Racine JS (2008) Nonparametric Econometrics: The np Package. Journal of 414 Statistical Software 27(5). URL http://www.jstatsoft.org/v27/i05/

Hayfield T, Racine JS (2017) Nonparametric kernel smoothing methods for mixed data types. 416 Package "np"

Halffter G (1987) Biogeography of the montane entomofauna of Mexico and Central 418 America. Annu Rev Entomol 32:95–114

Heilmann-Clausen J, Maruyama PK, Bruun HH, Dimitrov D, Læssøe T, Frøslec TG, 420 Dalsgaard B (2017) Citizen science data reveal ecological, historical and evolutionary factors shaping interactions between woody hosts and wood-inhabiting fungi. New

422 Phytol 212:1072–1082

Hegland SJ, Nielsen A, Lázaro A, Bjerknes AL, Totland Ø (2008) How does climate warming
424 affect plant-pollinator interactions? Ecol Lett 12:184–195

Hewitt G (2000) The genetic legacy of the Quaternary ice ages. Nature 405:907–913

426 Kantsa A, Raguso RA, Dyer AG, Olesen JM, Tscheulin T, Petanidou T (2018) Disentangling the role of floral sensory stimuli in pollination networks. Nature Comm 9:1041

428 Lara C (2006) Temporal dynamics of flower use by hummingbirds in a highland temperate forest in Mexico. EcoScience 13:23–29

430 Licona-Vera Y, Ornelas JF (2014) Genetic, ecological and morphological divergence between populations of the endangered Mexican Sheartail Hummingbird (*Doricha eliza*).
432 PLoS ONE 9:e101870

Licona-Vera Y, Ornelas JF (2017) The conquering of North America: dated phylogenetic and
434 biogeographic inference of migratory behavior in bee hummingbirds. BMC Evol Biol 17:126

436 Maglianesi MA, Blüthgen, Böhning-Gaese K, Schleuning M (2014) Morphological traits determine specialization and resource use in plant-hummingbird networks in the
438 Neotropics. Ecology 95:3325–3334

Maglianesi MA, Blüthgen, Böhning-Gaese K, Schleuning M (2015) Functional structure and
440 specialization in three tropical plant-hummingbird interaction networks across an elevational gradient in Costa Rica. Ecography 38:1119–1128

442 Malpica A, Ornelas JF (2014) Postglacial northward expansion and genetic differentiation between migratory and sedentary populations of the broad-tailed hummingbird
444 (*Selasphorus platycercus*). Mol Ecol 23:435–452

Marquitti FMD, Guimarães PR Jr., Pires MM, Bittencourt LF (2014) MODULAR: Software
446 for the Autonomous Computation of Modularity in Large Network Sets. Ecography 37:221–224

448 Martín González AM, Allesina S, Rodrigo A, Bosch J (2012) Drivers of compartmentalization in pollination networks. Oikos 121:2001–2013

450 Martín González AM, Dalsgaard B, et al. (2015) The macroecology of phylogenetically structured hummingbird-plant networks. Glob Ecol Biogeogr 24:1212–1224

452 Maruyama PK, Vizentin-Bugoni J, Oliveira GM, Oliveira PE, Dalsgaard B (2014) Morphological and spatio-temporal mismatches shape a Neotropical savanna plant-
454 hummingbird network. Biotropica 46:740–747

McGuire JA, Witt CC, Remsen JV Jr, Corl A, Rabosky DL, Altshuler DL, Dudley R (2014)
456 Molecular phylogenetics and the diversification of hummingbirds. Curr Biol 24:910–916

458 Morrone JJ (2010) Fundamental biogeographic patterns across the Mexican Transition Zone: an evolutionary approach. Ecography 33:355–361

460 Morrone JJ, Escalante T, Rodríguez-Tapia G (2017) Mexican biogeographic provinces: map and shapefiles. Zootaxa 4277:277

462 Navarro SAG, Townsend Peterson A, Gordillo-Martínez A (2002) A Mexican case study on a centralised database from world natural history museums. Data Sci 1:45–53

464 Oksanen J (2017) Vegan: an introduction to ordination. Package "vegan"

Olesen JM, Bascompte J, Dupont YL, Jordano P (2007) The modularity of pollination
466 networks. Proc Natl Acad Sci USA 104:19891–19896

Ornelas JF, Lara C (2015) Differential response to color task on resident and migratory
468 hummingbirds: a field test. Ethol Ecol Evol 27:257–378

Ornelas JF, González C, Espinosa de los Monteros A, Rodríguez-Gómez F, García- Feria LM
470 (2014) In and out of Mesoamerica: temporal divergence of *Amazilia* hummingbirds pre-dates the orthodox account of the completion of the Isthmus of Panama. J
472 Biogeogr 41:168–181

Ornelas JF, González de León S, González C, Licona-Vera Y, Ortiz-Rodriguez AE,
474 Rodríguez-Gómez F (2015) Comparative palaeodistribution of eight hummingbird species reveal a link between genetic diversity and Quaternary habitat and climate
476 stability in Mexico. Folia Zool 64:245–258

Ornelas JF, Sosa V, Soltis DE, Daza JM, González C, Soltis PS, Gutiérrez-Rodríguez C,
478 Espinosa de los Monteros A, Castoe TA, Bell C, Ruiz-Sanchez E (2013) Comparative phylogeographic analyses illustrate the complex evolutionary history of threatened
480 cloud forests of northern Mesoamerica. PLoS ONE 8:e56283

Poisot T, Stouffer DB, Gravel D (2015) Beyond species: why ecological interactions. Oikos
482 124:243–251

Rech AR, Dalsgaard B, Sandel B, Sonne J, Svenning JC, Holmes N, Ollerton J (2016) The
484 macroecology of animal versus wind pollination: ecological factors are more important than historical climate stability. Plant Ecol & Div 9:253–262

486 Ricklefs RE (1987) Community diversity: relative roles of local and regional processes. Science 235:167–171

488 Rodríguez-Gómez F, Gutiérrez-Rodríguez C, Ornelas JF (2013) Genetic, phenotypic and ecological divergence with gene flow at the Isthmus of Tehuantepec: the case of the
490 azure-crowned hummingbird (*Amazilia cyanocephala*). J Biogeogr 40:1360–1373

Rzedowski J (1965) Relaciones geográficas y posibles orıgenes de la flora de México. Bol
492 Soc Bot México 29:121–177

Stouffer DB, Bascompte J (2011) Compartmentalization increases food-web persistence. Proc
494 Natl Acad Sci USA 108:3648–3652

Sonne J, Martín González, et al. (2016) High proportion of smaller ranged hummingbird
496 species coincides with ecological specialization across the Americas. Proc R Soc B 283:20152512

498 Stiles FG (1978) Ecological and evolutionary implications of bird pollination. Am Zool 18:715–727

500 Stiles FG (1981) Geographical aspects of bird-flower coevolution, with particular reference to Central America. Ann Miss Bot Gard 68:323–351

502 Thuiller W, Münkemüller T, Lavergne S, Mouillot D, Mouquet N, Schiffers K, Gravel D (2013) A roadmap for integrating eco-evolutionary processes into biodiversity
504 models. Ecol Lett 16:94–105

Tylianakis JM, Laliberté E, Nielsen A, Bascompte J (2010) Conservation of species
506 interaction networks. Biol Conserv 143:2270–2279

Vizentin-Bugoni J, Maruyama PK, Sazima M (2014) Processes entangling interactions in
508 communities: forbidden links are more important than abundance in a hummingbird–plant network. Proc Royal Soc B: Biol Sci 281:20132397

510 Weinstein BG, Graham CH, Parra JL (2017) The role of environment, dispersal and competition in explaining reduced co-occurrence among related species. PloS One
512 12:e0185493

TABLES

514 Table 1. Hummingbird species and the traits examined in this study. Phylogenetic lineages were obtained from McGuire et al. (2014), biogeographical species distribution from their
516 observed community location, body mass and bill length from Arizmendi and Berlanga (2014) and from Carlos Lara's own measurements (marked with and asterisk *), degree of
518 endemism from Escalante (1993) and species migratory behavior from Arizmendi and Berlanga (2014).

Hummingbird species	Phylogenetic lineage	Biogeographical distribution	Bill length (mm)	Body mass (g)	Degree of endemism	Migratory behavior
Amazilia beryllina	Emerald	Widespread	18.71*	4.06*	Non endemic	Non migrant
Amazilia candida	Emerald	Neotropical + Transition	17.2	3.6	Non endemic	Non migrant
Amazilia cyanocephala	Emerald	Neotropical + Transition	21	5.5	Non endemic	Non migrant
Amazilia rutila	Emerald	Neotropical + Transition	21.75	4.75	Non endemic	Non migrant
Amazilia tzacatl	Emerald	Neotropical + Transition	21.25	5.35	Non endemic	Non migrant
Amazilia violiceps	Emerald	Widespread	22.5	5	Semi endemic	Local migrant
Amazilia yucatanensis	Emerald	Neotropical + Transition	21.25	3	Semi endemic	Local migrant
Anthracothorax prevostii	Mango	Neotropical + Transition	27.25	7	Non endemic	Non migrant
Archilochus alexandri	Bee	Widespread	18.75	3.65	Semi endemic	Long distance migrant
Archilochus colubris	Bee	Widespread	16.04*	5.36*	Non endemic	Long distance migrant
Atthis heloisa	Bee	Nearctica + Transition	12.32*	2.53*	Endemic	Non migrant
Calothorax lucifer	Bee	Nearctica + Transition	21.02*	3.86*	Semi endemic	Long distance migrant
Calothorax pulcher	Bee	Transition	17.9	2.85	Endemic	Non migrant
Calypte anna	Bee	Nearctica	17.25	3.6	Non endemic	Local migrant
Calypte costae	Bee	Nearctica	17	2.5	Non endemic	Local migrant
Campylopterus curvipennis	Emerald	Neotropical + Transition	27.3	5.8	Non endemic	Non migrant
Campylopterus hemileucurus	Emerald	Neotropical + Transition	27.8	11.9	Non endemic	Non migrant
Chlorostilbon auriceps	Emerald	Transition	14	3.25	Endemic	Non migrant
Chlorostilbon canivetii	Emerald	Neotropical + Transition	14.3	3.25	Non endemic	Non migrant
Colibri thalassinus	Mango	Widespread	19.71*	6.03*	Non endemic	Local migrant
Cynanthus latirostris	Emerald	Widespread	21.25	3.5	Semi endemic	Local migrant
Cynanthus sordidus	Emerald	Transition	29	4.5	Endemic	Non migrant
Doricha eliza	Bee	Neotropical + Transition	22.4	2.5	Endemic	Non migrant

Eugenes fulgens	Gem	Widespread	26.88*	7.65*	Non endemic	Local migrant
Eupherusa poliocerca	Emerald	Transition	17.8	4.85	Endemic	Non migrant
Heliomaster constantii	Gem	Neotropical + Transition	34	7.65	Non endemic	Non migrant
Heliomaster longirostris	Gem	Neotropical + Transition	34.5	6.8	Non endemic	Non migrant
Hylocharis leucotis	Emerald	Widespread	17.03*	3.95*	Non endemic	Local migrant
Hylocharis xantusii	Emerald	Nearctica	18	3.6	Endemic	Non migrant
Lampornis amethystinus	Gem	Transition	19.11*	6.98*	Non endemic	Non migrant
Lampornis clemenciae	Gem	Widespread	23.92*	8.39*	Semi endemic	Local migrant
Lamprolaima rhami	Gem	Transition	21.9	6.35	Non endemic	Non migrant
Lophornis brachylophus	Coquette	Transition	13	2.7	Endemic	Non migrant
Lophornis helenae	Coquette	Neotropical	11.3	2.7	Non endemic	Non migrant
Phaethornis longirostris	Hermit	Neotropical + Transition	43.2	5.75	Non endemic	Non migrant
Phaethornis striigularis	Hermit	Neotropical + Transition	21.55	2.65	Non endemic	Non migrant
Selasphorus calliope	Bee	Nearctica + Transition	14.5	2.5	Semi endemic	Long distance migrant
Selasphorus platycercus	Bee	Widespread	17.74*	3.73*	Semi endemic	Long distance migrant
Selasphorus rufus	Bee	Widespread	16.68*	3.65*	Non endemic	Long distance migrant
Selasphorus sasin	Bee	Neotropical + Transition	16.71*	3.59*	Semi endemic	Long distance migrant
Tilmatura dupontii	Bee	Transition	13.6	2.85	Non endemic	Non migrant

Table 2. Results from the non-parametric multiple regression with kernel variable estimation between species within and between module connectivity (*z* and *c* value, respectively) and their morphological and biogeographical traits. Regression was performed with the 41 hummingbird species and using the 5 studied variables. We used a local-linear kernel regression estimator, using a second-order Gaussian kernel function for the two continuous explanatory variables (bill length and body mass), an Aitchison and Aitken kernel function for the unordered categorical variable (biogeographical distribution) and a Li and Racine kernel function for the two ordered categorical variable (degree of endemism and migratory behavior). Bandwidths were computed using an adaptive k-nearest neighbor algorithm and selected through a least squares cross-validation (Hayfield and Racine 2008, 2017). Significance tests were performed with 399 bootstraps. Significant variables are marked in bold.

	z value		*c* value	
Goodness of fit (R^2)	0.730		0.699	
Standard error	0.101		0.039	
	Bandwidth	P value	Bandwidth	P value
Bill length	**36**	**0.040**	36	0.719
Body mass	**19**	**0.018**	28	0.276
Biogeographical distribution	**4.40e^{-07}**	**2e^{-16}**	**0.135**	**0.008**
Degree of endemism	0.589	0.155	1.000	0.145
Migratory behavior	**0.075**	**2e^{-16}**	**0.516**	**0.010**

FIGURES

534 **Figure 1**. Map of Mexico showing the different biogeographical regions conforming the Nearctical realm (in blue), the Neotropical realm (in orange) and Transition provinces (in
536 green) as defined by Morrone et al. (2017). Dots pinpoint the localities where the hummingbird-plant networks were collected. Note that some of the points may overlap.

538

Figure 2. Illustration of the Mexican bipartite meta-network. Hummingbirds in blue and
540 plants in orange, and the interactions between them in grey. The width of the species' bars represents species' number of interactions. Hummingbirds are also divided according to their
542 resulting modules. The picture shows a female *Selasphorus platycercus* visiting a flower of *Penstemon roseus*. Photo by Carlos Lara.

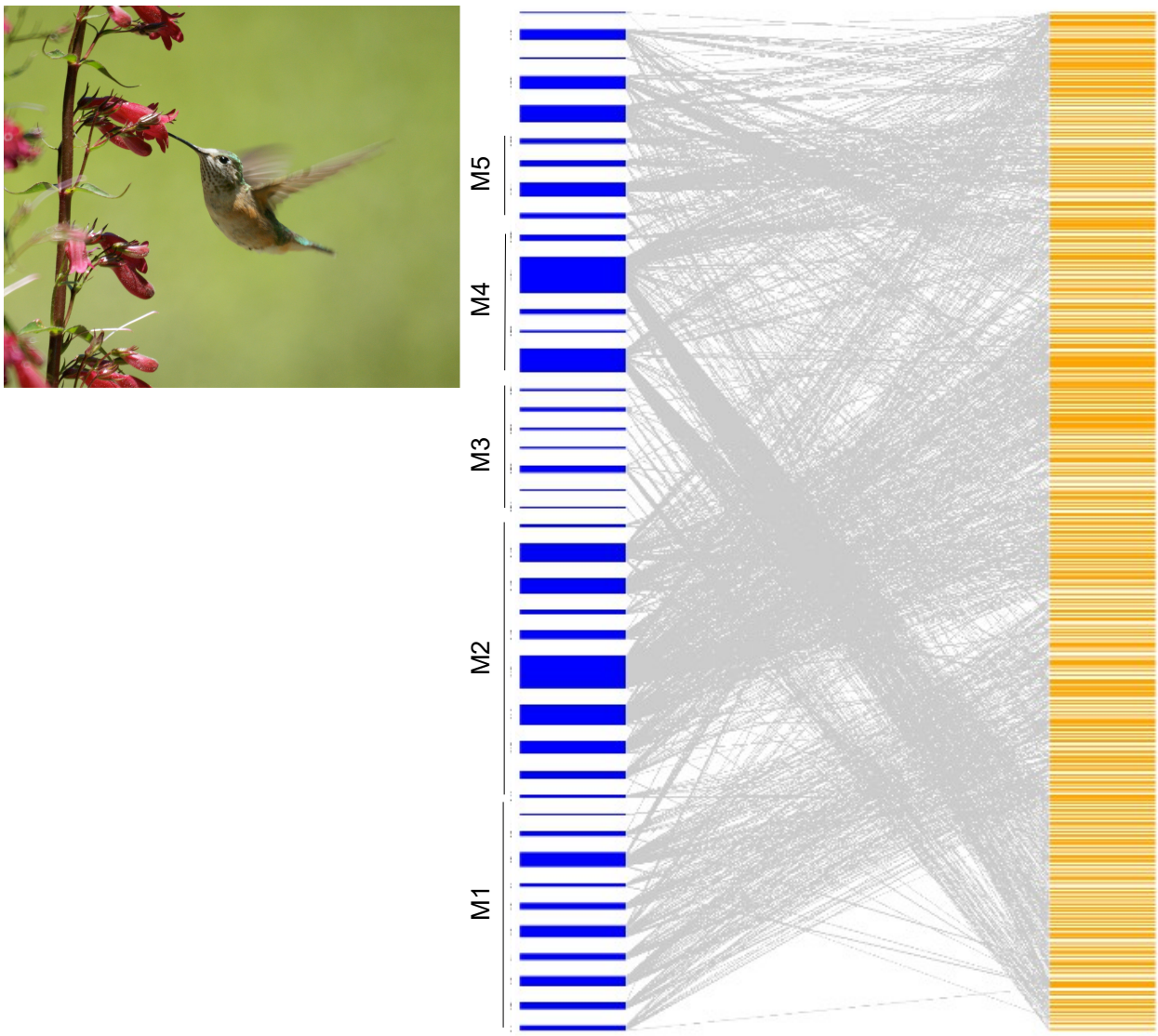
544

Figure 3. Results of the non-metric muldimensional scaling ordination of five hummingbird
546 species traits (bill length, body mass, biogeographical distribution, degree of endemism and migratory behavior). Ellipses in the NMDS indicate 95% confidence intervals around the
548 centroids of each group. Note that modules 6-10 (colored in different shades of red) are conformed of only one hummingbird species, as these hummingbirds appeared in different
550 modules in the different runs of the modularity algorithm. Notice also that these hummingbirds do not show biogeographical or morphological differences from
552 hummingbirds with constant module partners.

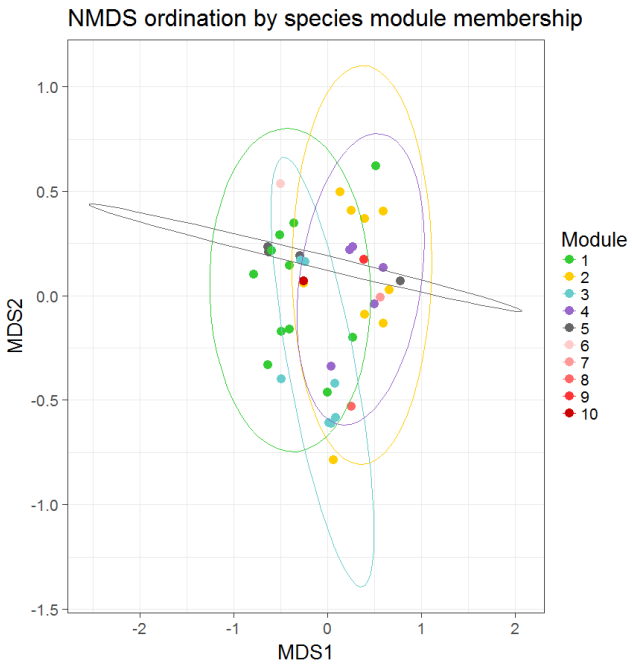
554 **Figure 4**. Plots illustrating the significant correlations between *z* and *c* values and migratory behavior (a,b), biogeographical distribution (c,d), bill length (e) and body mass (f) of
556 hummingbirds. Pirateplots show raw data as points, the median as a horizontal line surrounded by a Bayesian 95% Inference Highest Density Interval as a horizontal bar, and a
558 smoothed density bean surrounding the raw data points.

Figure 1

562 Figure 2.

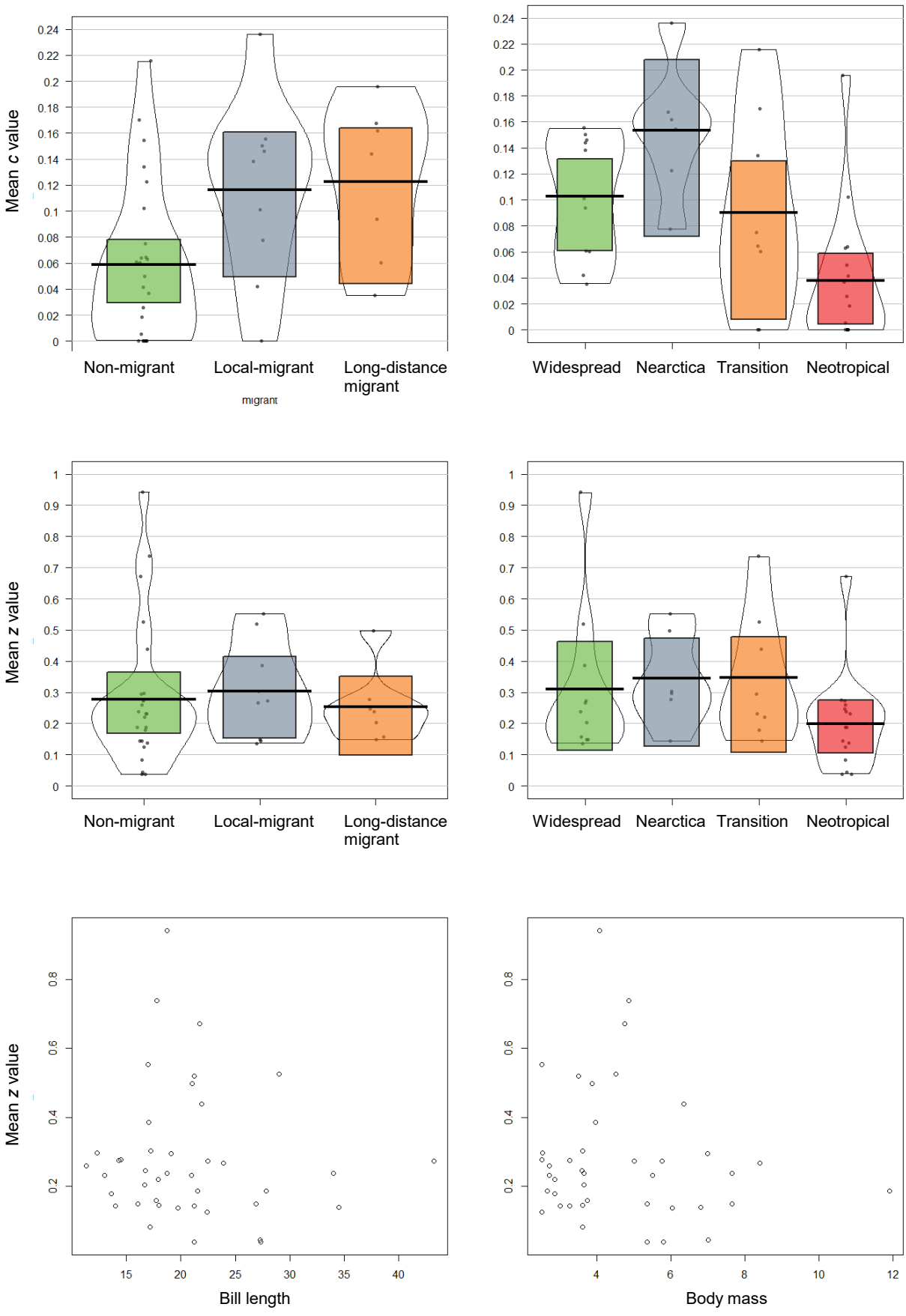


564 Figure 3



	Axis 1	Axis 2
Bill length	0.159	-0.249
Mass	0.122	-0.424
Biogeographical distribution	0.358	-0.013
Degree of endemism	-0.163	0.836
Migratory behavior	-1.041	-0.054

566 Figure 4.


Mean c value
0.24
0.22
0.2
0.18
0.16
0.14
0.12
0.1
0.08
0.06
0.04
0.02
0
Non-migrant
Local-migrant
Long-distance migrant
migrant
Widespread
Nearctica
Transition
Neotropical
Mean z value
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Bill length
15
20
25
30
35
40
Body mass
4
6
8
10
12

SUPPORTING INFORMATION

Appendix 1. Details about the Mexican biogeography and hummingbird fauna and biogeographical characteristics.

Mexico is an outstanding example of complex biogeographical patterns (Morrone 2010; Morrone et al. 2017). The Mexican Transition Zone (Halffter 1987), which marks the transition between the Neotropical and the Nearctic biota, is considered a critical area for understanding not just diversification in the region, but also the evolution of migratory systems of various animal species. This zone includes the Isthmus of Tehuantepec in southern Mexico, formed c. 3 Ma, and the Trans-Mexican Volcanic Belt (TMVB) across central Mexico, formed c. 10–7 Ma (Gómez-Tuena et al. 2007). The Isthmus of Tehuantepec divides mountain ranges along the Sierra Madre Oriental and Oaxaca from those in Chiapas and Guatemala. Its formation was followed by changes in sea levels caused by glaciation cycles, with rising sea levels and marine transgression during interglacials inundating much of the coastal plains and isolating montane habitats on either side (Barrier et al. 1998). At present, the lowlands in the area are occupied by dry scrubby habitats that are very different from the moist mountainous areas on either side. The TMVB was formed during four main episodes of volcanic activity from the middle-to-late Miocene to the Holocene (Gómez-Tuena et al. 2005), resulting in a continental magmatic arc of nearly 8000 volcanic chain of mountains (reaching over 4000 m above sea level), extending west to east and virtually cutting Mexico into northern and southern halves. The TMVB acts as an effective geographic barrier to the dispersal of most hummingbird species, producing abrupt environmental changes, which may explain the existence of such high number of endemic hummingbird species. Recent phylogeographic studies have shown that species level population divergence of terrestrial species post-dates Pliocene faulting and marine inundations across the Isthmus of Tehuantepec (Barber and Klicka 2010; Ornelas et al. 2013 and references therein).

The Mexican hummingbird fauna (including all North American species) began with a single invasion from South America by the common ancestor of the Bee and Mountain Gem clades ca. 12–14 million years ago (McGuire et al. 2014; Licona-Vera and Ornelas 2017). After this

598 invasion, there have been multiple independent invasions of North America by Emeralds,
Coquettes, Mangoes, and Hermits and single invasions by Brilliants and Topazes, presumably
600 all of which occurred prior to or after the Panamanian land bridge formation (McGuire et al.
2014; Ornelas et al. 2014). Species accumulation in North America proceeded slowly at first
602 and a rapid increase during the past 7 Ma, which reflects not only in situ diversification of
Mountain Gems and Bees, but also a heterogeneous diversification dynamics during the
604 history of hummingbirds and an extraordinary high rate of net diversification in the Bee clade
(McGuire et al. 2014), potentially linked to the evolution of migratory behavior (Licona-Vera
606 and Ornelas 2017). In the Nearctic-Neotropical migration systems, analyses of molecular data
suggest that many bird species colonized northern areas when they became available after the
608 Last Glacial Maximum (LGM) event (Hewitt 2000). For example, the ancestral sedentary
ranges of the Bee clade (such as *Selasphorus* species) expanded into northern latitudes
610 following the LGM, until they reached limits for residency imposed by the local seasonality
of the floral resources and migration was selectively favoured (Malpica and Ornelas 2014).
612 These migrations were followed by rapid radiations and local adaptations to both xeric and
humid conditions in different regions of Mexico, and produced both sedentary and migratory
614 populations (Licona-Vera and Ornelas 2017). In a phylogenetic framework, the repeated
evolution of long-distance migratory behavior is observed at different times in the radiation of
616 the Bee clade, highlighting the key role of the environment (local topographical features and
climatic changes) on processes of divergence and speciation. These repeated gains of
618 migration at the phylogenetic scale seem to have occurred linked to certain patterns of
climatic change during the Late Pliocene and Pleistocene glaciations, whereas the evolution of
620 long-distance seasonal migration within species seems to have occurred during the last
glacial-interglacial cycles of the Pleistocene (Rodríguez-Gómez et al. 2013; Malpica and
622 Ornelas 2014; Licona-Vera and Ornelas 2017).

Appendix 2. Table S2. Geographical and habitat details for each hummingbird-plant network.

Study #	Author	Mexican state	Main Vegetation type	Latitude	Longitude	Biogeographical province	Biogeographical realm
1	Rodríguez-Flores, C.I.	Jalisco	Cloud forest	19°34’14’’ - 19°37’30’’	104°14’49’’ - 104°18’16’’	Sierra Madre del Sur	Transition
2	Ortiz-Pulido, R.	Veracruz	Pine forest	19°29'59.86"	97° 8'12.08"	Trans-Mexican Volcanic Belt	Transition
3	Arizmendi, M.C.	Jalisco	Tropical deciduous forest	19° 30'	105° 03'	Pacific Lowlands	Neotropical
4	Arizmendi, M. C.	Jalisco	Cloud forest	19° 35'	104° 16'	Sierra Madre del Sur	Transition
5	Des Granges, J.- L.	Colima	Pine-oak forest	19°31'3.18"	103°37'5.55"	Trans-Mexican Volcanic Belt	Transition
6	Partida Lara, R.	Chiapas	Cloud forest	16º44'38"	92º40'15"	Chiapas Highlands	Transition
7	Arizmendi, M. C.	Guerrero	Pine-oak forest	17°19’53.1” - 17°25’47.8”	100° 09’ 56.1” - 100°11’48.5”	Sierra Madre del Sur	Transition
8	Lyon, D. L.	Oaxaca	Pine forest	17° 8'26.67"	96°41'21.55"	Sierra Madre del Sur	Transition
9	Arriaga, L.	Baja California Sur	Oak forest	24º-22º50'	109º60'-110º10'	Baja Californian	Nearctica
10	Reyna Bustos, O.	Jalisco	Tropical deciduous forest	21°45’08’’-21°44’50’’	103°15’	Pacific Lowlands	Neotropical
11	De la Cruz, F.	Oaxaca	Xeric shrubland	17°04’04’’	96°43’12’’	Sierra Madre del Sur	Transition
12	Jimenez Sierra, L.	Hidalgo	Xeric shrubland	20°45’26’’	98°57’08’’	Sierra Madre Oriental	Transition
13	Toledo, V.	Veracruz	Evergreen tropical forest	18°32’	95° 04’	Veracruzan	Neotropical
14	Van Devender, T.	Sonora	Foothills thorn scrubs	28°34'40"	109°33'09"	Sonoran	Nearctica
15	Van Devender, T.	Sonora	Tropical deciduous forest	28254'48"	109°11'31"	Sonoran	Nearctica
16	Van Devender, T.	Sonora	Oak woodland	28°22'18"	109°03'53"	Sonoran	Nearctica
17	Van Devender, T.	Sonora	Pine-oak forest	28°19'31"	109°02'00"	Sonoran	Nearctica

18	Martínez-García, V. 1	Hidalgo	Xeric shrubland	20°36'44"	98°44'54"	Sierra Madre Oriental	Transition
19	Martínez-García, V. 2	Hidalgo	Oak forest	20°40'31.7"	98°45'12.3"	Sierra Madre Oriental	Transition
20	Martínez-García, V. 3	Hidalgo	Pine-oak forest	20°41'45.82"	98°45'55.92"	Sierra Madre Oriental	Transition
21	Díaz-Valenzuela, R. 1	Hidalgo	Pine forest	20°11'11"	98°42'34"	Sierra Madre Oriental	Transition
22	Díaz-Valenzuela, R. 2	Hidalgo	Pine forest	20°41'45.82"	98°45'55.92"	Sierra Madre Oriental	Transition
23	Díaz-Valenzuela, R. 3	Hidalgo	Oak forest	20°41'45.82"	98°45'55.92"	Sierra Madre Oriental	Transition
24	Montgomerie, R. D.	Nayarit	Tropical deciduous forest	21°32'	105°17'	Pacific Lowlands	Neotropical
25	Lara, C.1	Tlaxcala	Pine forest	19°13'49.5"	98° 58' 19.67"	Trans-Mexican Volcanic Belt	Transition
26	Lara, C.2	Tlaxcala	Oak forest	19°17'36"	98° 14' 30"	Trans-Mexican Volcanic Belt	Transition
27	Lara, C.3	Veracruz	Cloud forest	19º30'	96º57'	Trans-Mexican Volcanic Belt	Transition
28	Díaz-Fisher 1	Puebla	Arid tropical scrubland	19°36'45"	96° 53' 45"	Sierra Madre del Sur	Transition
29	Arizmendi, M. C.	Puebla	Arid tropical scrubland	18°18'31"	97° 29' 25"	Sierra Madre del Sur	Transition
30	Díaz-Fisher 2	Puebla	Arid tropical scrubland	19°25'55"	96° 31' 53"	Sierra Madre del Sur	Transition
31	Puch Chávez, R.	Campeche	Evergreen tropical forest	18°21'	89° 49'	Yucatán Peninsula	Neotropical
32	Puch Chávez, R.	Campeche	Evergreen tropical forest	18°32'	89° 47'	Yucatán Peninsula	Neotropical
33	López Segoviano, G.	Sinaloa	Oak forest	23°34'16"	105°50'15"	Sonoran	Nearctica
34	Medina-van Berkum, P. et al.	Yucatán	Xeric shrubland	21°37’23.4” - 21°34’19”	88°07'42.3" - 88°06’00.9”	Yucatán Peninsula	Neotropical
35	Vidal-Hernández, W. J.	Estado de México	Pine-oak forest	19°48'2.8"	99° 31' 15.1"	Balsas Basin	Neotropical

36	Martínez-Roldan, H.	Tlaxcala	Xeric shrubland	19°23´31”	97°55´49”	Trans-Mexican Volcanic Belt	Transition
37	Bautista-Salazar, L.	Querétaro	Xeric shrubland	20º 30´- 20º 55	100º 17´ - 100º 36´	Chihuahuan Desert	Nearctica

624 References:

ID number	Data Source Reference
1	Rodríguez-Flores CI (2009) Dinámica de las estrategias de forrajeo por néctar en colibríes (Aves: Trochilidae) en la Reserva de la Biosfera Sierra de Manantlán. (Jalisco, México). MSc Thesis, Universidad Nacional Autónoma de México.
2	Ortiz-Pulido R, Díaz R (2001) Distribución de colibríes en la zona baja del centro de Veracruz, México. Ornitol Neotrop 12: 297–317
3	Arizmendi MC (1987) Interacción entre los colibríes y su recurso vegetal en Chamela, Jalisco. BSc Thesis, Universidad Nacional Autónoma de México.
4	Arizmendi MC (1994) Interacciones ecológicas múltiples: el caso del sistema mutualista colibríes-plantas y el ladrón de néctar *Diglossa baritula* (Passeriformes: Aves). PhD Thesis, Universidad Nacional Autónoma de México.
5	Des Granges JL (1978) Organization of a tropical nectar feeding bird guild in a variable environment. Living Bird 17: 199–236.
6	Lara RP, Enríquez PL, Rangel-Salazar JL, Lara C, Ico, MM (2012) Abundancia de colibríes y uso de flores en un bosque templado del sureste de México. Rev Biol Trop 60: 1621–1630
7	Arizmendi, M. C. Unpublished data.
8	Lyon DL (1976) A montane hummingbird territorial system in Oaxaca, Mexico. Wilson Bull 88: 280–299
9	Arriaga L, Rodriguez-Estrella R, Ortega-Rubio A (1990) Endemic hummingbirds and Madrones of Baja: Are they mutually dependent? Southwest Nat 35: 76–79.
10	Reyna Bustos O (2008) Utilización de los recursos florales por colibríes en el bosque tropical caducifolio de la barranca de Colimilla, Jalisco, México. MSc Thesis, Universidad de Guadalajara.
11	De la Cruz F (2011) Estudio preliminar de la avifauna nectarívora del Jardín Botánico de la Cd. De Oaxaca de Juárez, Oaxaca. BSc Thesis, Universidad Tecnológica del Valle de Oaxaca.
12	Jiménez-Sierra L, Reyes S (2003) Las Cactáceas de la Barranca de Metztitlán. In M.A. Armella, M.L. Yánez y E. Sandoval (Eds.): Metztitlán: Lugar de la Luna y de las Maravillas. Universidad Autónoma Metropolitana.México. 53–77 p.
13	Toledo VM (1975) La estacionalidad de las flores utilizadas por los colibríes de una selva tropical húmeda en México. Biotropica 7: 63–70.
14 - 17	Van Devender TR, Calder WA, Krebbs K, Reina-G AL, Russell SM, Russell RO, Nabhan GP (2004) Hummingbird plants and potential nectar corridors for the rufous hummingbird in Sonora, Mexico. Conserving migratory pollinators and nectar corridors in western North America. Univ. Arizona Press and Arizona-Sonora Desert Museum, Tucson, pp.96–121
18 - 20	Martínez–García V (2006) Interacciones colibrí–planta en tres tipos de vegetación de la Reserva de la Biosfera Barranca de Metztitlán, Hidalgo, México. BSc Thesis, Universidad Autónoma del Estado de Hidalgo, Pachuca. 58 p.
21 - 23	Díaz–Valenzuela R (2008) Análisis descriptivo del sistema colibrí–planta en tres niveles de las escalas espacial, temporal y en la jerarquía ecológica en un paisaje mexicano. PhD Thesis. Centro Iberoamericano de la Biodiversidad, Alicante. 60 p.
24	Montgomerie RD, Gass CL (1981) Energy limitation of hummingbird populations in tropical and temperate communities. Oecologia, 50(2): 162–165
25	Lara C (2006) Temporal dynamics of flower use by hummingbirds in a highland temperate forest in México. Ecoscience 13: 23–29.
26	Lara, C. Unpublished data
27	Lara, C. Unpublished data
28, 30	Díaz-Fisher A (2002) Determinación de la abundancia y distribución de los colibríes en la Reserva de la Biosféra Tehuacán-Cuicatlán durante el periodo primavera-verano. BSc Thesis, Universidad de las Américas-Puebla. 42 p.
29	Arizmendi MC, Espinosa de los Monteros A (1996) Avifauna de los bosques de cactáceas columnares del valle de Tehuacán–Cuicatlán. Acta Zoológica Mexicana (nueva serie) 67:25–46
31, 32	Puch-Chávez R (2012) Flora visitada por colibríes en selvas maduras y sitios

deforestados en Calakmul, Campeche. BSc Thesis, Universidad Autónoma de Campeche. México

33 López-Segoviano G (2012) Comportamiento territorial y preferencias de forrajeo del colibrí migratorio Selasphorus rufus dentro de un sitio invernal. MSc Thesis, Universidad Nacional Autónoma de México. 50 p.

34 Medina-van Berkum P, Parra-Tabla VP, Leirana-Alcocer JL (2016) Recursos florales y colibríes durante la época seca en la Reserva de la Biosfera Ría Lagartos, Yucatán, México. Huitzil, 17: 244–250

35 Vidal-Hernández, W. J. Unpublished data

36 Martínez-Roldan, H. Unpublished data

37 Bautista-Salazar, L. Unpublished data

Appendix 3. Adjacency matrix for the Mexican meta-network. Hummingbird species in columns, plants in rows, 1 depicts at least an observed interaction somewhere in the Mexican territory, 0 otherwise. Hummingbirds are ordered by module membership, as result of running 30 times a modular partition in MODULAR (Marquitti et al. 2014). Hummingbirds are placed in the same module when in 87% of the times (i.e. more than 26 out of the 30 runs of the modularity algorithm) result in the same module, and are labeled NA when they have no constant module partners.

	M1	M1	M1	M1	M1	M1	M1	M1	M1	M1	M1	M2	M2	M2	M2	M2	M2	M2	M2	M2	M3	M3	M3	M3	M3	M3	M3	M4	M4	M4	M4	M5	M5	M5	NA	NA	NA	NA	NA
	Amazilia candida	Amazilia tzacatl	Amazilia yucatanensis	Anthracothorax prevostii	Archilochus colubris	Campylopterus curvipennis	Campylopterus hemileucurus	Chlorostilbon canivetii	Doricha eliza	Lophornis helenae	Phaeotornis striigularis	Atthis heloisa	Colibri thalassinus	Eugenes fulgens	Hylocharis leucotis	Lampornis amethystinus	Selasphorus calliope	Selasphorus platycercus	Selasphorus rufus	Selasphorus sasin	Calothorax pulcher	Chlorostilbon auriceps	Eupherusa poliocerca	Heliomaster longirostris	Lophornis brachylophus	Phaethornis longirostris	Tilmatura dupontii	Amazilia violiceps	Calypte anna	Calypte costae	Cynanthus latirostris	Cynanthus sordidus	Amazilia cyanocephala	Amazilia rutila	Archilochus alexandri	Heliomaster constantii	Amazilia beryllina	Calothorax lucifer	Hylocharis xantusii	Lampornis clemenciae	Lamprolaima rhami
Acanthaceae sp1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Acanthaceae sp2	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Aechmea bracteata	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Agave angustifolia	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0
Agave difformis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Agave garciamendozae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Agave inaequidens	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	
Agave ishtmensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Agave salmiana	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	1	0	0
Agave sp1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0
Agave sp2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Agave sp3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Agave sp4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Agave sp5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Agave sp6	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1
Agave striata	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0
Aloe vera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Anisacanthus andersonii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0
Anisacanthus thurberi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Anneslia peninsularis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	
Annona longiflora	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0
Antigonon leptopus	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	1	0	0	0	0
Antirrhinum majus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0
Aphelandra aurantiaca	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arbutus xalapensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	
Arcostaphylos pungens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Asclepias curassavicus	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	1	0	0	0
Asthiantus vimidalis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0
Bauhinia erythrocalyx	0	0	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bauhinia sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Bauhinia variegata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Bernoullia flammea	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Bessera elegans	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0
Bessera tenuiflora	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	
Bomarea edulis	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0
Bougainvilla spectabilis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0
Bougainvillea cf spectabilis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bourreria pulchra	0	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

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Neobuxbaumia scoparia	0	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nerium oleander	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Nicotiana glauca	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	1	0	1	1	0	1	0
Odontonema callistachyum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oenothera sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Operculina pteripes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Opuntia decumbens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Opuntia excelsa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Opuntia ficusindica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Opuntia fuliginosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0
Opuntia gosseliniana	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Opuntia imbricata	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0
Opuntia karwinskiana	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	0	0
Opuntia pilifera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0
Opuntia sp1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Opuntia sp2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0
Opuntia sp3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Opuntia sp4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Pachycereus hollianus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0
Palicourea padifolia	1	1	1	1	0	1	1	1	0	0	0	1	1	1	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0
Passiflora membranacea	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Paullinia sessiliflora	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Penstemon barbatus	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0
Penstemon gentianoides	0	0	0	0	1	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Penstemon hartwegii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Penstemon kunthii	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Penstemon perfoliatus	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Penstemon roseus	0	0	0	0	1	0	0	0	0	0	0	0	1	1	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0
Penstemon sp	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Petrea volubilis	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phaseolus coccineus	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	1	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0
Phaseolus sp1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phaseolus sp2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phisoodium adenodes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Phitecoctenium cruciferum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0
Pilocereus alensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Pinguicula moranensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Piscidia piscipula	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pitcarnia palmeri	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Pithecellobium mangense	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Plumeria rubra	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0
Polianthes geminiflora	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Prunella vulgaris	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pseudobombax palmeri	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Psittacanthus calyculatus	1	0	0	0	0	0	1	1	0	0	0	1	0	1	1	0	0	1	1	0	0	0	1	1	1	0	1	1	0	0	1	0	1	1	1	1	1	1	0	0	0
Psittacanthus mayanus	0	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Psittacanthus palmeri	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Psittacanthus ramiflorus	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0
Quamoclit coccinea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Ribes ciliatum	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ribes dugesii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ribes sanguineum	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Roldana angulifolia	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rondeletia sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rosa sp1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Rosa sp2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Rubus adenotrichos	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Ruellia inundata	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Russelia flavoviridis	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Russelia sp	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

| | | |

| | | |

Appendix 4. Results from the modularity analysis. Modularity was calculated in MODULAR (Marquitti et al. 2014) using Barber's metric for bipartite networks (Barber 2007), with simulated annealing as the searching algorithm and following the recommended program settings: an initial temperature of 2.0, a cooling factor of 1.01, and an iteration factor of 1 (Marquitti et al. 2014). Barber's modularity divides the matrix into an a priori undefined number of modules using matrix's eigenvalues, minimizing the number of links between modules while maximizing within-module connectance (Barber 2007). We estimated the significance of each run against 100 null matrices obtained with MODULAR's Null Model 2, which creates matrices with the same number of species and interactions as the empirical one, and in which species interaction probability is based on their observed connectivity (Bascompte et al. 2003; Marquitti et al. 2014). As MODULAR uses an iterative searching algorithm, we investigated the robustness of the resulting modular partition by running the analysis 30 times using different seed set numbers. The resulting 30 partitions showed similar levels of modularity but differed in the resulting number of modules (Table S3.1). Hence, we further explored the species composition of the modules in the different runs. Species composition of modules was relatively constant, with all but five of the hummingbird species being placed over 87% of the runs together in the same module (that is, in 26 out of the 30 runs). This threshold value for establishing modules was chosen through a hierarchical agglomerative cluster analysis of dissimilarity data (Figure S3.1). Supporting this partition, hummingbirds with variable module partners were not randomly scattered but tended to be placed together with specific modules (Figure S3.1) and showed no differences in any of the studied traits with species forming constant groups (Table 1, Figure S3.2).

References

Müllner D (2017) Fast hierarchical clustering routines for R and Phyton. Package "fastcluster"

Zhao S, Guo Y, Sheng Q, Shyr Y (2016) An improved heatmap package. Package "heatmap3"

Table S4.1. Results from the 30 runs of the MODULAR (Marquitti et al. 2014) modularity analysis. Notice that the resulting number of modules varies between 5 and 8. Modularity values average M=0.466, with a standard deviation of SD=0.004. All runs were significantly modular when compared against matrices of same number of species and interactions as the empirical one, and where species have a probability of interaction derived from their observed connectivity (NM2).

Run ID	Number of resulting modules	Modularity value	NM2 p-value
1	7	0.471	0
2	6	0.467	0
3	5	0.466	0
4	7	0.464	0
5	8	0.464	0
6	6	0.473	0
7	5	0.462	0
8	7	0.471	0
9	7	0.464	0
10	8	0.464	0
11	6	0.463	0
12	6	0.464	0
13	8	0.464	0
14	8	0.464	0
15	6	0.465	0
16	5	0.473	0
17	6	0.461	0
18	8	0.471	0
19	5	0.467	0
20	6	0.474	0
21	7	0.461	0
22	5	0.464	0
23	7	0.464	0
24	6	0.462	0
25	5	0.458	0
26	5	0.471	0
27	7	0.466	0
28	6	0.464	0
29	6	0.466	0
30	6	0.458	0

Figure S4.1. Heatmap illustrating the frequency each pair of hummingbird species was placed in the same module in each modularity run. The modularity algorithm was run 30 times. Clustering analysis was performed with a fast hierarchical and agglomerative routine of dissimilarity data from the *fastcluster* package in R (Müllner 2017) resulting in five clusters. Arrows mark the five hummingbird species without constant partners. Heatmap compiled in the *heatmap3* package in R (Zhao et al. 2016).

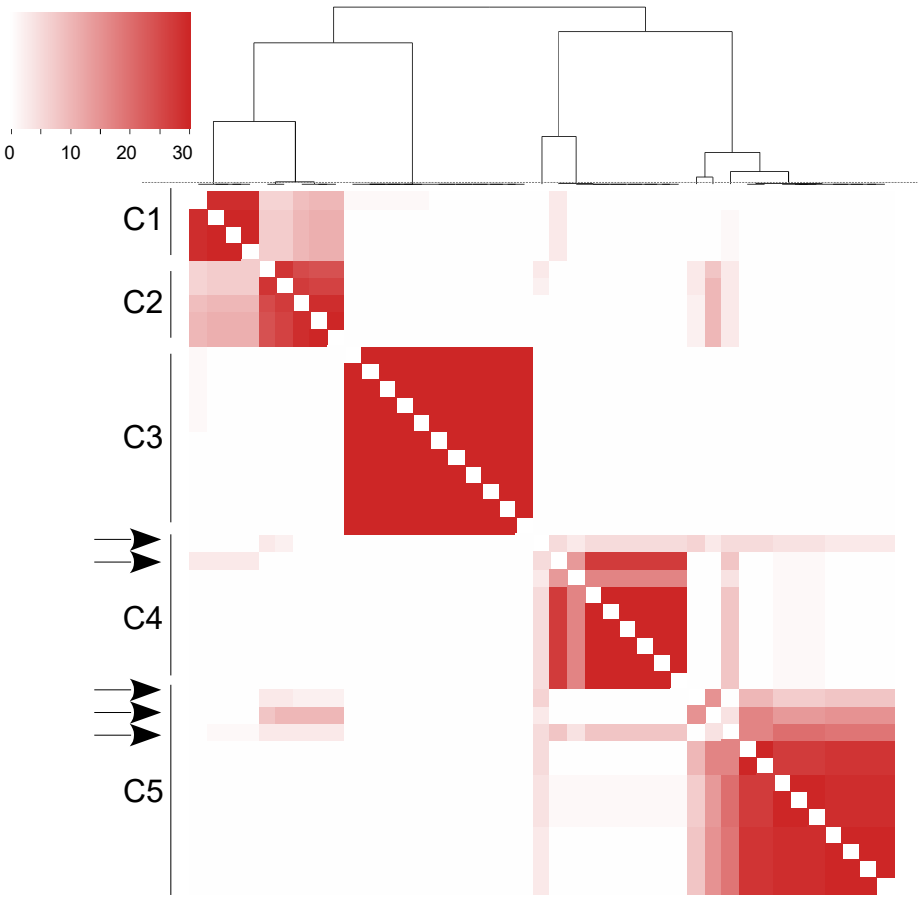
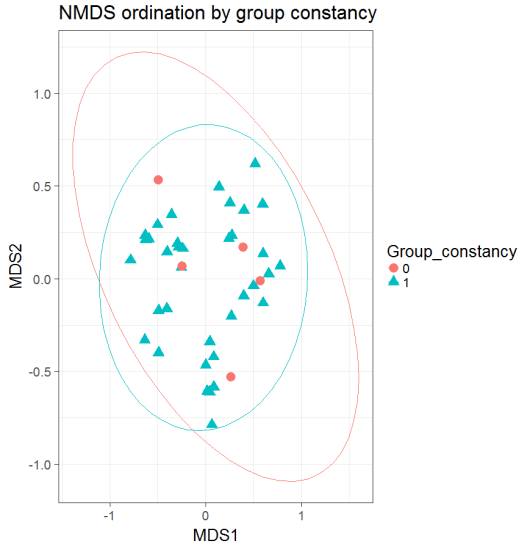
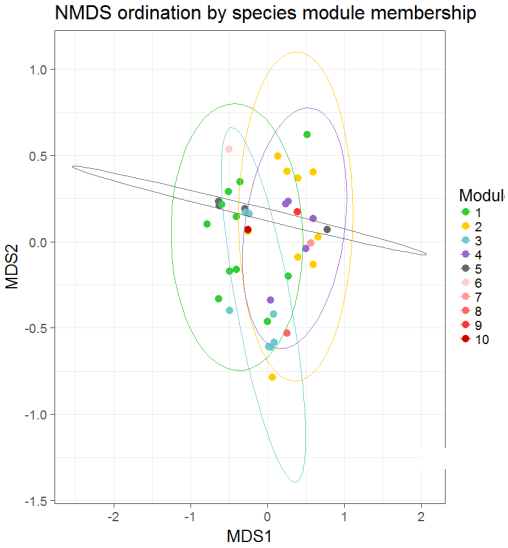


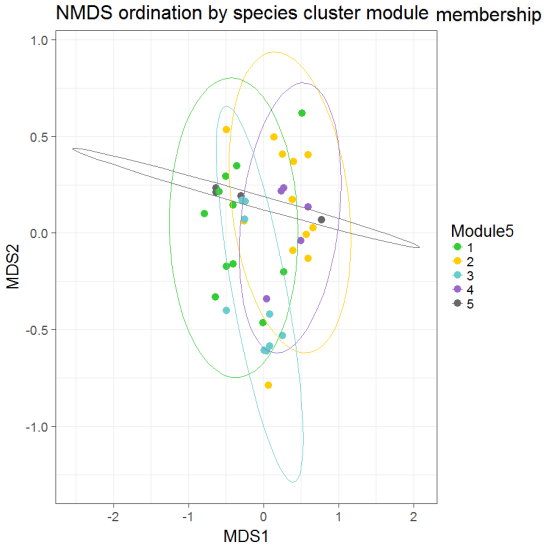
Figure S4.2. Results of the non-metric muldimensional scaling ordination of five hummingbird species traits (bill length, body mass, biogeographical distribution, degree of endemism and migratory behavior). The illustration shows (a) how hummingbirds without fixed module-partners do not differ in traits from hummingbirds with fixed module partners, and (b,c) the lack of significant differences when considering modules conformed of only constant partners (bottom left, the partition showed in the main text) and when considering modules derived from the cluster partition (bottom right). Ellipses in the NMDS indicate 95% confidence intervals around the centroids of each group. Note that analyzing only constant groups of partners or clusters result in virtually identical ellipses.

	Axis 1	Axis 2
Bill length	0.159	-0.249
Mass	0.122	-0.424
Biogeographical distribution	0.358	-0.013
Degree of endemism	-0.163	0.836
Migratory behavior	-1.041	-0.054





Goodness of fit = 0.426, p-value = 0.001



Goodness of fit = 0.345, p-value = 0.001

692 Appendix 5. Partial regression plots for the asymptotic errors of the non-parametric multiple regression with kernel smoothing analysis.

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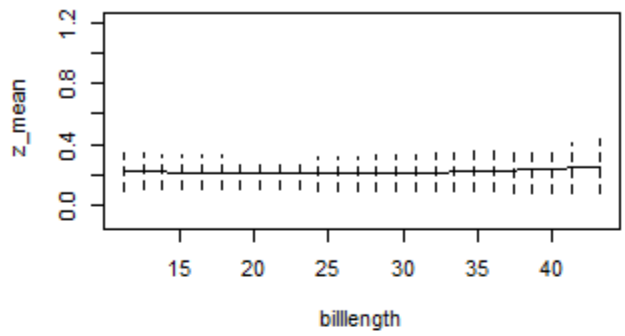
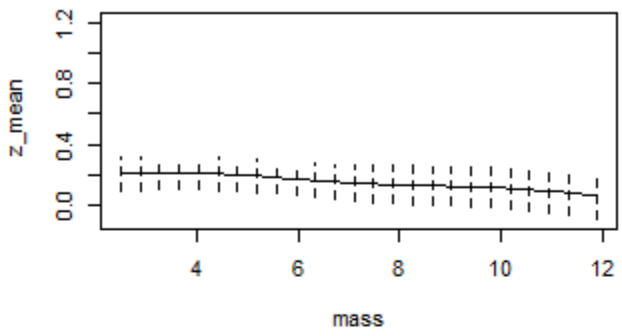
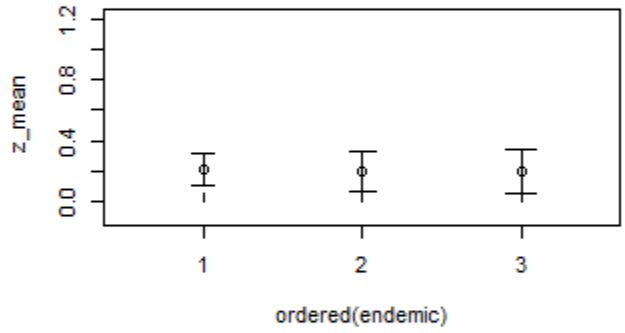
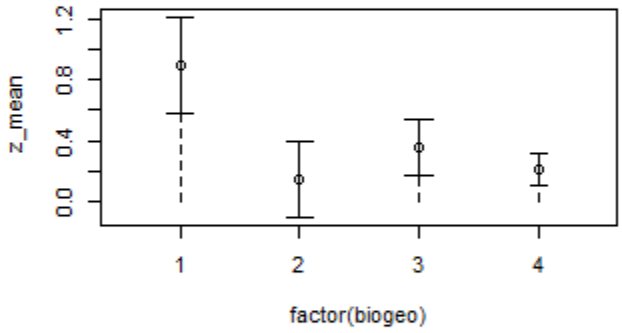
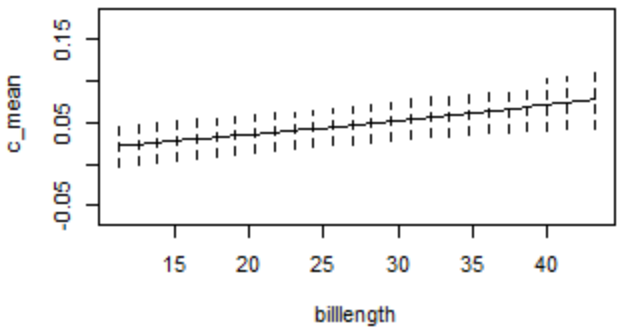
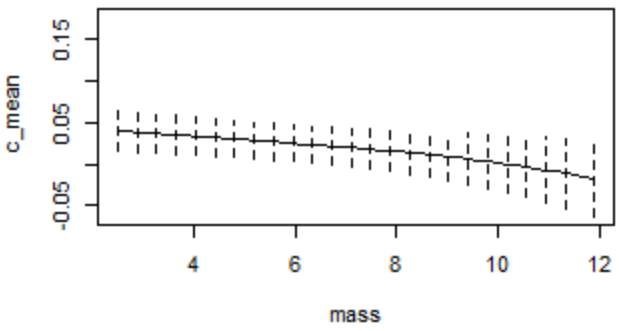


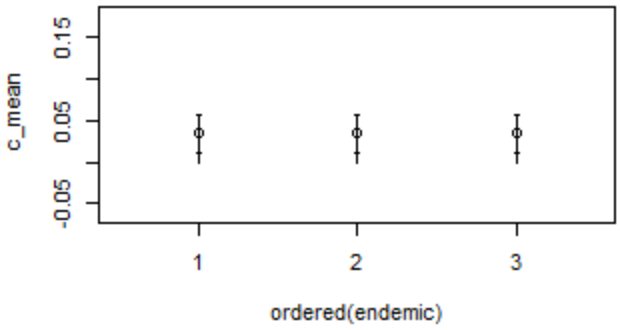


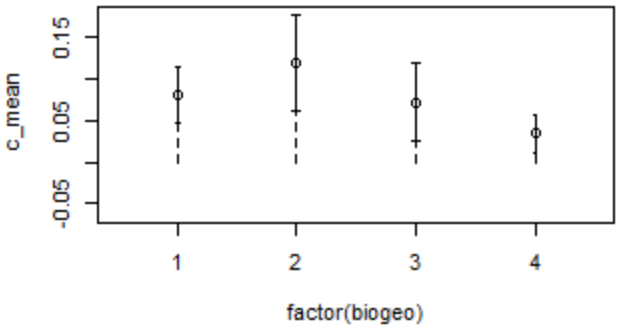


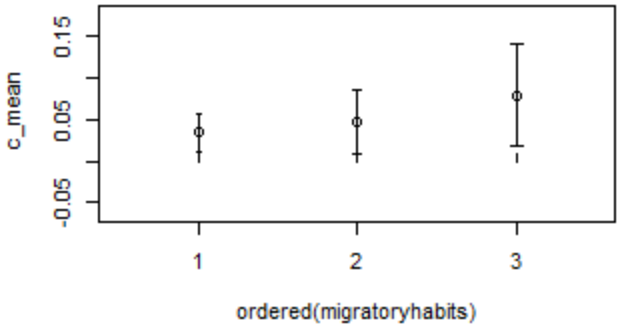



c_mean
0.15
0.05
-0.05
15
20
25
30
35
40
billlength


c_mean
0.15
0.05
-0.05
4
6
8
10
12
mass


c_mean
0.15
0.05
-0.05
1
2
3
ordered(endemic)


c_mean
0.15
0.05
-0.05
1
2
3
4
factor(biogeo)


c_mean
0.15
0.05
-0.05
1
2
3
ordered(migratoryhabits)

Appendix 6. Differences in average *c* values in the various hummingbird phylogenetic lineages (KW $X^2 = 13.751$, df = 5, p-value = 0.017).